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THE ANT COLONY AS A COMPLEX SYSTEM

Ants are more than a hundred million years older than humans, and they cover the land surface of the planet. Probably people have always watched ants, and probably they have always asked the same question: How can ants get anything done when no one is in charge? Whoever wrote Proverbs 6:6 put it this way: “Look to the ant, thou sluggard—consider her ways and be wise. *Without chief, overseer or ruler*, she gathers the harvest in the summer to eat in the winter.” The history of our understanding of ant behavior is the history of our changing views of how organizations work.[1]

There have been times when it was impossible to imagine an ant colony without a leader. The scientific study of ants began when natural history joined the rest of the emerging sciences in the eighteenth century. It was already clear that ants live in colonies, consisting of one or more reproductive females, while the rest are sterile females. Among bees, the reproductive female in a colony was called the ‘queen,’ and the females who do not reproduce called ‘workers,’ by Charles Butler in *The Feminine Monarchie, or the Historie of Bees*, in

1609.[2] These observations of bees were extended to ants in the eighteenth century by the French naturalist Réaumur. Like his contemporaries, such as Maeterlinck, writing about bees, Réaumur described ants as a group of subordinate laborers happy to serve their monarch. Although these names imply a hierarchy that in other times, both before and since Réaumur, was known not to exist, the names 'queen' and 'worker' have stuck. Two hundred and fifty years later, scientists have identified more than 11,000 species of ants, and they all live in colonies of females, with some sterile and some reproductive.

The 150 years that followed Réaumur's vision of ants as contented subjects of a benevolent queen brought worldwide political upheaval, raising questions of whether monarchy is the most natural form of society. This period (1750–1900), in which evolutionary biology was born, generated thinking about democracy, revolution, freedom, and cooperation, all of which influenced the ways we see the natural world, including ants. In a lively discussion in the Ecole Normale in Paris in 1795, year 3 of the French Revolution, Daubenton, a professor of natural history, argued that there is no royalty in nature—for example, the queen bee does nothing more than lay eggs. His colleague Latreille wrote in 1798 that the ants in the colony are not really subjugated workers; instead, the colony has "a single will, a single law" based on the love each ant feels for the others.[3]

Throughout the nineteenth century, colonial expansion put Europeans in contact with the stunning diversity of the tropics. Evolutionary biology and ecology began out of the effort, which is still under way, to explain this diversity. The idea of natural selection as the outcome of ecological processes, what

Darwin called "the struggle for survival," gradually became the basis for the scientific study of all organisms.

Skipping over many crucial discoveries about the life cycles, physiology, and natural history of insects generally and ants in particular, we could locate the beginning of contemporary scientific work on ants with the efforts of W. M. Wheeler.[4] Wheeler borrowed from Herbert Spencer the term "superorganism," comparing the ant colony not to a kingdom but to a single organism, with the queen and workers all acting as cells that contribute to the life of one reproducing body. Because ants do not make more ants, but instead colonies reproduce to make more colonies, a colony is in fact an individual organism in the ecological sense. As the gametes of different trees join, when pollen meets ovary, to make the seeds that produce new trees, so the reproductives of different colonies mate to produce new colonies.

With the colony as superorganism, the queen is no longer in charge, and we return to the puzzle of how such a system could be organized. This issue resonated with general questions about cooperation in animals raised in the early twentieth century by authors like Kropotkin, a Russian aristocrat turned anarchist. Do the ants work for the good of the colony, in the same way that cells work for the good of the body, and is this because evolution favors those who cooperate?

Despite all the transformations in our thinking about society, it is still very difficult for us to describe ant society without depicting it as hierarchically organized. Someone is always in charge. Either the bad guys are in charge, and the lowly workers feel oppressed and rebellious, or the good guys are in charge, and the lowly workers are happy. During the

Cold War, ants were models of a totalitarian society. In *The Book of Merlyn* by T. H. White,[5] Merlin transforms the young Arthur into an ant and sends him to work in a desolate tunnel with loudspeakers blaring allegiance to an ant Big Brother and walls plastered with signs reading "Everything not forbidden is compulsory." More recently, movies such as *Antz*, *It's a Bug's Life*, and *The Ant Bully* show the colony as a corporation with more or less disgruntled workers. These changes continue to be mirrored in scientific ideas about ants.

In the 1950s and 1960s, evolutionary biology took up an economic, free-market perspective with a vengeance. Anyone who did not see natural selection as promoting the gain, or profit, of the individual, was considered to be soft-headed and out of touch. Wheeler's ideas about the superorganism were scorned as soft-headed, "an appealing mirage," and "a panchreston of little relevance" (from a 1968 paper by E. O. Wilson).[6]

Wilson's pioneering work on ants, to which he brought his immense gift for making accessible to everyone the fascination of nature, was the starting point for modern research on social insects. Drawing on ideas from the nascent sciences of cybernetics, which led to the development of computers, he created a vision of colony behavior as a mechanical process, a "factory constructed inside a fortress."[7] Each component, the ant, was genetically programmed to do its task. An ant of a certain type would perform a certain task over and over, directed by its genes and responding to fixed chemical signals. Most ants see poorly, and they rely on chemical cues. An ant has many glands in its body that secrete chemicals. Working with Bert Holldobler, Wilson set out to find the meaning of each chemical—for example, one chemical may signal alarm, and another may mark a trail to be used by foragers. In their view, the chemical signals were the triggers for the ant's preprogrammed instructions to kick in. This view of the ant colony culminated in a set of mathematical optimization models. Oster and Wilson's 1978 book, *Caste and Ecology in the Social Insects*,[8] outlines how such a system would be tuned by natural selection to produce, in each species, just the right mix of ants to do each task as required by the environment. The queen was not in charge, but natural selection had stepped in instead, setting up the system in advance so that each ant does what needs to be done.

The idea of a perfectly adapted distribution of worker sizes was one answer to the question of how ant colonies could work without central control. More generally, this question is an instance of one of the fundamental puzzles of biology. In the early twentieth century, developmental biologists argued bitterly about another version of the same question: What determines the fate of cells in an embryo? All cells are formed from the division of one or two parent cells, so they all have the same genes. What then tells one cell to become liver and another to become bone? Does one organism, or one cell on its own, have inside it whatever determines its development, like the ancient idea of the preformed homunculus inside each sperm, or instead do the cells require interactions with each other to determine what they will become? It happened that the choice of systems used by developmental biologists in the late nineteenth century, sea urchins or frog embryos, helped to polarize this debate: the two sides had chosen organisms that differed greatly in how soon cell interactions become important, so that in one, isolated cells could go on to develop, and in the other, they could not.

Different outcomes of particular experiments, depending on choice of methods, have also shaped our ideas about ants. This was crucial to the course of my own work. I began to study ants as a graduate student in the early 1980s. The prevailing research program on ants at that time was set by the idea of the adaptive distribution of worker sizes in a colony, each type genetically programmed to respond to particular cues and perform particular tasks.

I was looking for an example of a system in which to investigate organization without hierarchical control. I was interested in embryonic development, but I chose ants instead because I learn best by watching, and it is a lot easier to watch ants than to observe cells as they divide and differentiate in a growing embryo.

Of the many species of ants, I chose harvester ants because one of my professors in graduate school at Duke, Fred Nijhout, told me of a well-known study by Wilson that concluded that for harvester ants, oleic acid is a necrophoric pheromone, causing any ant treated with oleic acid to be taken "live and kicking" to the refuse pile, or midden.[9] (There are many species of seed-eating or harvester ants, but in this book I use 'harvester ant' to mean my favorite, *Pogonomyrmex barbatus.*) I tried to repeat the experiment and found that ants did take bits of paper treated with oleic acid to the midden, but only at times when they were taking other things, like dead ants, to the midden. Harvester ants eat seeds, and many seeds contain oleic acid. When ants were taking other food into the nest, they also took oleic acid into the nest. Apparently, oleic acid functions either as garbage or as food, depending on what the workers that encounter it are doing.[10] When I sent my manuscript to Wilson to ask for comments, he told me that in his experiments, the ants treated with oleic acid had been chilled to keep them motionless. They were live but not really kicking, which might be why other ants took them to the midden.

The results of this study, the first chapter of my dissertation, took me in a direction orthogonal to the prevailing view of ant behavior. An ant's response to a chemical cue was not fixed, but depended on what the ant was doing. Then what determined what the ant was doing?

When I began to work on harvester ants, the closest place to find them was in a nature reserve next to the Army base at Fort Bragg, North Carolina. One day, after weeks of preparation, I had an experiment set up with little bits of paper soaked in oleic acid placed carefully around some nests. A group of soldiers landed their helicopter nearby to see what I was doing, producing a local gale that scattered the paper and the ants everywhere. I decided to find another place to work. I chose the Southwestern Research Station in southeastern Arizona, because all the other harvester ant species in the United States are in the southwest. When I went there for the first time, I fell in love with the desert. I grew up near the ocean and found the big sky and the desert wind coming across huge distances somehow familiar. I have returned there almost every summer since that first trip in 1981, to follow the same population of harvester ant colonies.

I've probably watched more ant colonies for longer than any other scientist, and for longer than most ant colonies have watched each other. Looking at the same harvester ant colonies week after week and year after year, I noticed that behavior changed. An ant's moment-to-moment response to a chemical cue depended on what it was doing right then.

A colony's response to its neighbors depended on what happened last week. Eventually, I realized that a colony's behavior changed over the years, as the colony grew older and larger. More and more, my questions were not about what ants do, but why ants and colonies change what they do.

As I finished graduate school and moved into postdoctoral research, my work on harvester ants showed that individuals switch tasks in response to changes in the environment and interactions with other ants; an ant's behavior is not simply a set of fixed responses to chemical signals.

In his 1980 book, *Gödel Escher Bach,*[11] Douglas Hofstadter asked us to think of distributed processing systems as being like ant colonies. It turns out that this vivid analogy does not do justice to the ants. My experiments began to show that ant colonies display even more dramatic emergent behavior than the computer simulations that in the 1980s transformed engineering. Today the use of 'ant' algorithms is a thriving industry in computer science, artificial intelligence, and robotics, and the use of network theory informs our understanding of ant behavior. It is clear that ant colonies make collective decisions, similar to the ones that keep schools of fish and swarms of insects together. Such decisions dictate not only how ants move around, but also how colonies find the resources and maintain an environment in which to begin, grow, and reproduce. What exactly is the similarity between an ant colony and a computer program, or an artificial brain?

Recently, I gave in to several months of intense lobbying by my (then) 12-year-old son, and we drove to a dusty and remote former Air Force base in southeastern California for the DARPA Urban Challenge. DARPA (Defense Advanced Research Projects Agency) is the Pentagon's military research unit, and this event is part of an effort to encourage research leading to the development of vehicles that can navigate using moment-to-moment responses to their own sensors, without any need for remote control. There were 11 robotic vehicles in the contest. Each had to navigate a designated route through the streets of the Air Force base, including turns, parking, and changes of lane. Each of the robotic vehicles was followed by another vehicle, driven by a person, and other vehicles were driven around as well. The problem for each robotic car was to avoid bumping into any other cars, adjusting its movement in response to information from various sensors mounted on its exterior. The winner was the robotic vehicle with the fewest infractions of the California driving code.

To understand what a 'complex biological system' is, it helps to compare such systems with the collection of robots in the DARPA Urban Challenge. An engineer's view would emphasize the similarities. In this cybernetic view, each component, whether an ant, a cell in an embryo, or a neuron, has a mission. It accomplishes its mission using the input it gets from various sensors. To understand such a system, the problem is merely to figure out what sensory cues each component uses. For example, in the 1980s view of ants, the forager is told by its genes to go out on a food-collecting mission, pick up the scent of a particular pheromone trail, follow it, collect the food, and return home.

An ant colony and a group of robotic vehicles have in common some of the processes that determine not what happens when they interact, but whether they interact at all. For both ants and vehicles, whether any two meet depends on how they all move around. Even for the 11 vehicles in the Urban Challenge, it would be hopelessly complicated to predict where any two vehicles were likely to interact, and this was the reason to hold the event, a multimillion-dollar experiment, in the first place. Many small contingencies determined which of the robotic vehicles had to pass another, or when one had to wait for another to back out of its parking space before moving forward to park itself. In fact, there was one collision during the 6-hour event. One robotic vehicle edged into the right lane of a roundabout and then stopped. A second robotic vehicle came along in the left lane, but moved toward the right lane of the roundabout just as the first robotic vehicle moved forward, and the two collided. At this point, all the other robotic vehicles were offered the opportunity to pause, and they all did. So when the first robotic vehicle stopped in the roundabout, it set off a series of events that eventually affected all the other vehicles and changed their subsequent encounters.

There are always dense webs of contingency in systems of interacting parts. In the circulation of wind around the earth, the movement of molecules in a glass of water, the fluctuations of the stock market, the speed and reach of the Internet, or the six degrees of separation between any two people on earth, the effects of actions of one component ripple out to others. When one ant does something that involves another and changes the positions of those two ants, or how long they stay in the same place, this will eventually influence the positions of all the other ants. This is what makes complex systems complex. But the complexity of complex biological systems is not what makes living systems unique.

One way that living systems are unique, so obvious that it's easy to forget, is that they cause their own development and activity. For example, a basic difference between a collection of robots and an ant colony is that people make the robots, while ant colonies are made by other ant colonies. We intervene in biological processes, sometimes spectacularly, as when we clone sheep or administer vaccines, and in countless other ways so frequent and essential that we don't even think of them as interventions, as when we eat or plant seeds. But our interventions merely alter ongoing processes, such as the development of a sheep's egg or the distribution of nutrients around a body—processes that we do not make or control. Human designers are behind everything a robot does. In an ant colony, there's nobody behind anything.

The ways that ants respond to interaction allow them to do on their own what the robots can do only at our instruction. Interactions with other ants determine what an ant does, and what the ant does modifies its environment, including its interactions, and this in turn modifies its subsequent interactions—and the whole process runs itself. This is true of all living systems. In a developing embryo, each cell's fate depends on its interactions with other cells. Inside a cell, which genes turn on at a certain time is a response to changing chemical gradients and contact with other cells, and what genes are turned on determines what the cell produces and how it influences the local chemical environment, which feeds back to turn genes on and off.

In an ant colony, a forager leaves the nest on a mission, to collect food. Interaction sets up the forager's mission in the first place, since it is stimulated to leave the nest by returning foragers, and interactions it has later on, such as an encounter with an alarmed ant, can change its mission and send it back into the nest without food. For the robotic vehicles in the DARPA challenge, in contrast, interaction could not change the mission, which was to drive around without bumping into anything; it was merely a possible source of failure.

This book is an introduction to the ant colony as a complex biological system, but not a general introduction to ant behavior. It presents a single idea about ants: that the behavior of ant colonies arises from dynamical networks of interaction. The book starts with the moment-to-moment behavior of ants within colonies and then scales up, ending with the evolution of ants over more than a hundred million years. Chapters 2 and 3 are about colony organization and the role of interaction networks in regulating the behavior of colonies. Chapter 4 is on the function of colony size, which varies among species and also changes as a colony develops and grows. Chapter 5 discusses ant ecology, the relations of ant colonies with neighbors of the same species and with other species. Chapter 6 summarizes the little we know about the evolution of colony behavior, and chapter 7 concludes by outlining the prospects for general models of colony organization.

This book is based on the idea that an ant colony's behavior is guided by a pulsing, shifting web of interactions, in which the pattern of interactions is more important than the content. This idea came out of my early work, and inevitably here I draw most on my own work and the ants I know best. Ideas about collective behavior in general, and networks of interaction in particular, have begun to sprout everywhere, and there are many compelling examples of these ideas applied to ants that I left out to keep the book short. There are countless excellent studies of many other fascinating aspects of ant behavior that are not mentioned here at all.

The series that includes this book is produced by the Santa Fe Institute, which has done much to nurture complex-systems thinking. The Santa Fe Institute grew out of the realization that biologists, physicists, and chemists, all studying different systems, are discovering analogous processes. The big questions about ant colony behavior are the same ones we have to ask about the behavior, ecology, and evolution of any biological system, and the limits to what we know about ants are set as much by how we frame the problem as by the number of person-hours spent getting the answers. This book maps out an approach to learning more about ants.